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ROOTS, THE HIDDEN HALF IN STRESSED ENVIRONMENT

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The root as it grows below ground supports and anchors the plant body. It likewise performs significant roles in water uptake, efficient acquisition of minerals from the growth medium, modification of the rhizosphere, and in association with the soil microflora. The simple structure of the root makes it suitable not only for studying growth and morphogenesis but also serves as a model system for biochemical studies and in biotechnology. Under adverse conditions of the environment, roots are able to carry out morphogenetic and physiological adaptation. This paper presents our studies and some of others on how the root acclimates when exposed to various abiotic stresses experienced both by itself and the shoot.

Key Words: abscisic acid, acclimation, compact soil, carbon dioxide, ethylene, oxygen, phosphorus, root meristem, salinity, UV-B, water logging, zinc

Abbreviations: AVG – aminoethoxyvinyl glycine; GUS gene - glucorunidase gene; KP – Kinandang Patong; LEA – late embryogenesis abundant; LMN – Lueb Mue Nahng; NPT – new plant type; UV-B- Ultraviolet B

Roots which evolved as an underground structure are exposed to the complex, competitive and hostile environment of the soil. The presence of a vast array of organisms from soil microorganisms to worms, ants and/or mice can change root growth and physiology. Nevertheless, root systems of vascular plants are successful in acquiring water and minerals in a limited and variable environment. A relatively forgotten function of the root is its mechanical role for anchorage, supporting the shoot system in a soil substrate. Its root strength, for example, is important in reducing incidence of lodging in crops.

Roots are simple structures containing relatively few cell types. All developmental stages are represented in a continuum along the length of the root. Root cells are arranged in a column along the longitudinal axis and cell files back to the meristem region. A cross-section anywhere behind the root tip reveals several concentric cell layers. The latter are likewise continuous with the layers of the hypocotyl (Chasan 1993). With these attributes, roots serve as a model for systems within the plant for studying problems of organization, cyto-differentiation, ultra-structural organelle function and biotechnology. A mathematical model of nutrient uptake (Clarkson 1985), a

Variation in Root Growth

Root growth is influenced by many stimuli, such as gravity, light and hormones, and again because of its simple structure, the root is ideal for studying the cellular and molecular basis of plant responses to these effectors. The roots of many dicots can be induced to proliferate indefinitely in culture by infecting with *Agrobacterium*, potentially aiding biochemical studies (Chasan 1993). We found that in transgenic plantlets of a Japonica rice cultivar, it is the root of regenerated calli that first showed the expression of GUS gene (Wang 1992) and in transformed potato plant, it was clearly manifested in the root meristem (Fu and Park 1995). In soil-grown plants, gradients exist along the root and the rhizosphere for mineral nutrients, water availability, oxygen status, pH, bulk density and temperature. Such gradients often affect root growth and physiology.

There is a wide variation in root growth, geometry and architecture among plant species which has been linked with acquisition of water and minerals (Lynch 1995; Marschner 1995). Genotypic differences in root length and some root apical characters are exemplified here between a rice hybrid and its immediate parent and that of different cultivars (Table 1). Although the root length in hybrid is only 4% longer than its immediate parent, longer meristem with greater number of dividing cells, earlier root hair differentiation and higher dry matter production were found in the hybrid. These findings suggest that root apical characters can be a measure of early expression of hybrid vigor. This proposal is strengthened by the positive correlation of root meristem size to high grain GA-like levels in hybrids (Miranda and Alejar 1993). On the other hand, roots of the new plant type (NPT) were 59.9% longer than a conventional cultivar IR-72 (Table 1). Although meristem length of NPT is half the size of IR 72, it exhibits greater number of dividing cells. Significant differences in root density, dry matter partition to roots, root surface area and root diameters were reported between F1 hybrid and IR-72 (Yamauchi and others 1991).

Table 1. Differences in root growth and root apical characters of 6-day-old rice seedlings of hybrid (n=10) and its immediate parent (n=10), a conventional cultivar, IR72 (n=30) and a new plant type (NPT) (n=30).

Root Parameter	Rice Cultivar			
	Parent	Hybrid	IR-72	NPT
Root length (mm)	85	120	74	177
Dry weight (mg)	110	140	68	160
Meristem length (µm)	452	490	387	188
Root hair zone (µm)	2036	1492	1190	930
Mitotic index	7.2	7.6	6.9	9.1

Acclimation Responses of Roots to Abiotic Stress

Deleterious effects of most environmental stresses are often experienced first by the root systems. The following presents some of the results of our investigation on how roots acclimate when exposed to light, lack of oxygen, waterlogging, mineral disorder, soil compaction, salinity, ultraviolet-B (UV-B) radiation and elevated CO_2 and/or high temperature. Acclimation here refers to responses which improve performance or survival or tolerance to the modified environment. Table 2 shows that there is likewise genotypic variation in response of rice to the stress-induced inhibition of root elongation. There is a wide range of values from 12.0% reduction when zinc is deficient to 99.9% at low oxygen levels and apparently reduction is greater in sensitive cultivars. However, promotion of root growth in some species is possible which otherwise is inhibitory to other crops (Table 3). For example, incorporation of rare earths, lanthanum and cerium, or chromium in soil can inhibit seedling root elongation of mungbean whilst promoting the same in tomato and pechay. Difference on the effect of the duration of contact with these elements on early root growth of cabbage has been reported by Alejar and others (1988a) which showed that the 10 ppm

Table 2. Genotypic variation in stress-induced inhibition of root elongation in contrasting rice cultivars. Values are expressed as % of controls.

Stress Factor	Rice Cultivar Tolerant	Rice Cultivar Sensitive
	%	%
Hypoxia	89.5	99.9
Ethylene inhibitor (AVG)	82.3	76.8
NaCl	72.2	96.1
Compact soil	71.6	70
Zn toxicity	84.6	89.2
Zn deficiency	13.1	12.0
UV-B	35	24.4
White light	70.3	-

concentration of the elements fared below that of the 5 ppm level in root elongation in case of cerium and lanthanum. Nevertheless, both concentrations stimulate root growth. With chromium treatment, root extension was lower than that in untreated roots.

Table 3. Promotion/inhibition of root elongation of seedlings exposed to some stress factor. Values are expressed as % of controls.

Species/stress	Inhibition	Promotion
	%	%
Barley		
compact soil	60	
NaCl	69	
ethylene	43	
Tomato		
waterlogging	48	
lanthanum 10 ppm		95
cerium 10 ppm		8
chromium 10 ppm		41
Mungbean		
lanthanum 10 ppm	14	
cerium 10 ppm		8
chromium 10 ppm	46	
Pechay		
lanthanum 10 ppm		42
cerium 10 ppm		17
chromium 10 ppm		32
Pepper		
lanthanum 10 ppm	2	
cerium 10 ppm	18	
chromium 10 ppm	84	
Azolla sp.		
P-deficiency		9
white light	50	
yellow light	32	

Light and Oxygen

Roots grow in darkness such that when exposed to white light, growth is inhibited by 25.4% in rice and 50.1% in barley seedlings (Wilkins and others 1978). When seeds germinate, it is the radicle that emerges first and is very sensitive to oxygen availability. Our studies in rice show that at 5% oxygen, coleoptile growth is evident but gave an almost zero radicle emergence in sensitive cultivar (Table 1). These conditions of depleted low oxygen supply is most experienced during direct-seeding practice on lowland irrigated soils. Hypoxia (or oxygen deficiency) is often found in roots surrounded by a layer of water in flooded soil. It could also occur in root apices and stele. Indeed stele of submerged roots experienced anoxic (absence of oxygen) zones even if the cortex is at ambient O_2 (Armstrong and Becket 1987) since endodermis and stele have a lower diffusivity to oxygen than does the cortex. When this situation applies to the apical meristem, where oxygen consumption per unit volume of tissue is greatest, there is inhibition of not only respiratory metabolism but also of dependent growth processes. The mathematical model of oxygen diffusion to roots helps explain the potential role of secondary wall thickening in hypodermis of rice in conserving oxygen that is diffusing down the roots from the leaves. This conservation improves the diffusion of oxygen to the root apical meristems so that growth can continue in an anaerobic medium (Drew and Stolzy 1991). Our results on root apical characteristics (Table 4) showed that inhibition at 10% O_2 on size of meristem was 30.6% in IR72 compared to 19.0% in Azucena and that earlier differentiation of root hair was observed in Azucena. These differential responses to low O_2 suggest that Azucena can better adjust to low oxygen supply as shown by the much lower reduction in root elongation and meristem size than the same in IR72. Mature rainfed rice cultivars, e.g. Azucena, are reported to have thicker and denser roots which penetrate deeper into soil layers (Vergara 1973).

Although root growth of rice seedlings is totally inhibited at 5% oxygen (Table 4), it is believed that cell viability can be maintained for some days. Many studies have shown that maintenance of root growth in poorly aerated conditions is favored by several distinct physiological and biochemical attributes particularly of rice roots. First, rice roots have a highly aerenchymatous cortex in which oxygen can diffuse and serve as stored oxygen which minimizes the risk of anaerobiosis in root apices, growing zone and phloem transport system. Second, a small amount of ethylene was trapped within the root cortex by water thereby promoting root extension growth. Third, certain groups of cells retain their ability to divide and form root primordia in the absence of oxygen. Fourth

Table 4. Root length and apical characters in seedlings of contrasting rice cultivars grown in hypoxic environment. Data are means of 30 measurements.

		Rice Cultivar	
Root Parameter	**% O_2**	**IR-72 Irrigated**	**Azucena Rainfed**
Root length (mm)	5	0	0.2
	10	1.1	2.7
	21	11.5	25.1
Meristem length (µm)	5	0	0
	10	384	496
	21	553	612
Root hair zone (µm)	5	0	0
	10	3410	3854
	21	1035	1441

is induction of pyruvate decarboxylase activity (Rivoal and others 1997) for better energy metabolism. The following are also likely to occur in rice roots as observed in other crops: induction of alcohol dehydrogenase activity as in maize (Johnson and others 1994) and *Arabidopsis* (Porterfield and others 1997); increase in lactate dehydrogenase as in maize (Christopher and Good 1996); increase in sucrose synthase as in tomato roots (Germain and others 1997) or decrease in hexokinase activity so that only sucrose is broken down in glycolysis (Ricard and others 1998). These enzyme changes under limiting O_2 supply maintain glycolysis and fermentation contributing to energy metabolism and viability. This can also likely be accompanied by increased levels of pyrophosphate dependent phosphofructokinase similar to that exhibited by hypoxically grown coleoptile (Valdez 1995). Recently, Biemelt and others (1998) reported higher total levels of ascorbate and glutathione in wheat roots in response to highly reducing conditions prevailing under hypoxia and anoxia and hence also an acclimation response of anaerobic roots.

Waterlogging, Ethylene and Abscisic Acid

In waterlogged rice fields, when about 90% of soil pores become water filled rather than gas filed (Cannell 1977), roots and aerobic soil microorganisms begin to asphyxiate. When poorly aerated, development of gas space within the root cortex referred to as aerenchyma is stimulated in rice and was also reported for maize (Jackson 1985). Indeed, many workers have demonstrated the close association between survival of roots in anoxic surroundings and the existence of aerenchyma connecting with above ground parts. Not only does it allow the entry of oxygen in the root but also oxidizes the likely reduced toxic compounds in waterlogged root environment.

Ethylene is known to induce aerenchyma formation (Jackson 1985) and stimulate rice root extension. Our study demonstrated that exposure of pre-germinated rice seedlings to 0.1 to 10 $\mu l\ L^{-1}$ ethylene proportionately enhanced root elongation (Table 5). Evidently in the presence of an ethylene inhibitor, aminoethoxyvinylglycine (AVG), there was a 70% to 80% inhibition of root length (Table 2). In contrast, ethylene inhibits elongation of roots of many species (Fig. 1). In well aerated solutions, elongation can be faster when exposed to small concentration of ethylene. However, further increases above a certain value can bring about inhibition. These differential responses to increased ethylene are determined by endogenous ethylene production. In rice, less ethylene is produced such that more exogenous ethylene is needed to supplement this to bring about inhibition. It has been calculated that the slow rate of ethylene production of rice roots will restrict the extent of ethylene accumulation in roots under water to growth-promoting concentrations. This may be of acclimatic significance to rice under hypoxic environment.

Ethylene and abscisic acid (ABA) are the hormones known to mediate stress responses. Increases in the level of these inhibitors have been reported in response to stress. Levels of hormones have been proposed as metabolic indicator of stress tolerance whether stress-induced or not (Alejar 1985). For example, high ABA levels detected in roots of droughted plants increased root conductivity to water, hence,

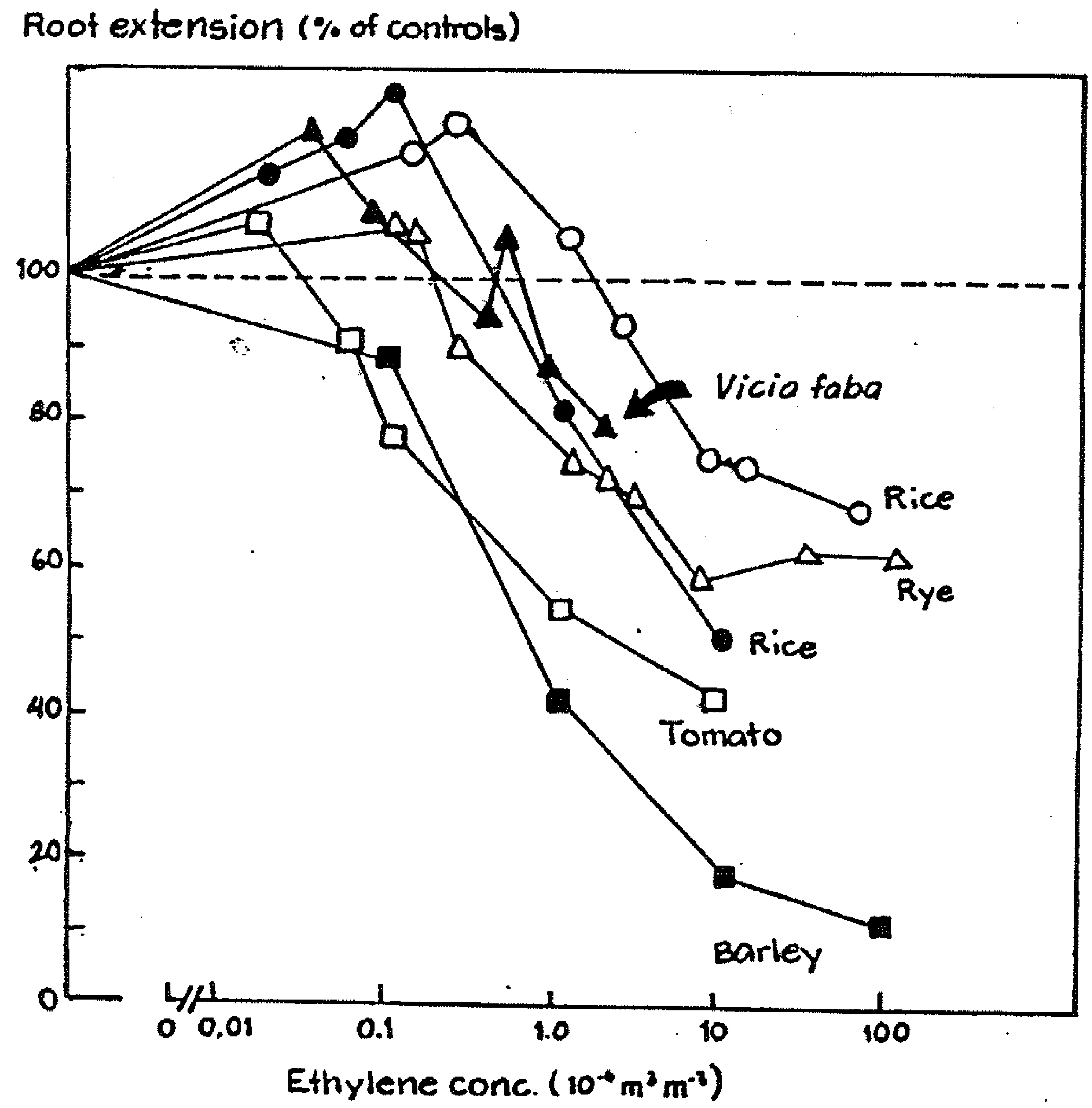

Fig. 1. The effect of increasing ethylene concentration on root elongation of some crop species (Jackson 1985)

maintaining water balance (Glinka and Reinhold 1971). This mechanism has been more commonly observed in drought-tolerant cereals (Alejar 1985). Wu and others (1994) have shown that exogenous ABA application maintains root elongation at low water potential. It is known that ABA regulates gene expression of stress proteins. Often, high levels of dehydrins and LEA proteins are detected in tolerant than sensitive cultivars of water-stressed (Chandler and Robertson 1994) or salt-stressed roots (Moons and others 1995). Contrary to the above findings, non-ABA mediation of dehydrin induction was reported in water-stressed roots of soybeans (Whitstitt and others 1997). Similarly, water deficit stimulates protein kinase as shown in water-stressed roots of maize (Conley and others 1997).

Table 5. The effect of ethylene on root elongation in germinating salt-tolerant and intolerant rice cultivars. Data are means of 20 measurements.

	Rice Cultivar	
Ethylene $\mu l\ L^{-1}$	**Salt Tolerant**	**Salt Intolerant**
0	18.8	9.9
0.1	15.7	10.8
2	14.1	12.0
5	19.2	13.5
10	23.7	15.3

Our data on waterlogging of some crops like barley, wheat, pea and tomato revealed reduction in root length (or total root length) by 14%, 41%, 52% and 89%, respectively.

In tomato the reduction in root growth (89%) by waterlogging for 5 days is coupled with an increase in ABA by as much as 16 and 18 times, respectively, of the bound and free form of the inhibitor (Alejar 1980). High ethylene release from the rhizosphere of waterlogged tomato seedlings was also detected compared with nil amounts in the non-waterlogged plants. On the other hand, high ethylene production in rice seedlings is correlated with salt tolerance in rice (Khan and others 1987).

Salinity

Figure 2 shows the proportionate decreases in root length with increasing salt concentration. The salt-tolerant cultivar, KP, appears to exhibit lesser reduction in growth than the sensitive LMN. Meristem length of salt-treated roots was markedly depressed by 300% in sensitive and by 50% in tolerant cultivar compared with controls (Table 6). The size of the apical meristem depends upon the balance which exists between cell proliferation by mitotic division in meristem and the onset of cell elongation at the proximal edge of the meristem. NaCl appears to alter this balance against cell proliferation, particularly in the salt-sensitive cultivar (Alejar and Davies 1995). In addition to continually producing daughter cells, most root apical meristems are indeterminate and must maintain themselves indefinitely. NaCl may have caused determinate growth and for individual cells, the transition from cell division to elongation is an all-or-nothing step (Bradford and Trewavas 1994). We believe that the mediation of ethylene in salt-stressed roots is at the early cellular events in the root apex (Alejar and Davies 1995). Ethylene has been shown to alter the orientation of microtubules (Roberts and others 1985). Reorientation of these may alter the plane of cell division in the root meristem which may, in turn, affect meristem length.

Typically, roothairs appear 2.5 mm back from the root tip. NaCl causes formation of root hairs closer to the meristem in salt-sensitive cultivar (Table 6). If this is so, one would expect a shorter zone of cell elongation. Thus it seems that such precocious cell differentiation may be a common feature of stress situations where root growth and cellular activity in the meristem is depressed. We also observed a massive proliferation of root hairs in salt-treated rice roots where, in some cases, the entire root was covered by a dense mass of roothairs. The same response has been found in a number of species upon exposure to ethylene (Reid 1995). In Table 6, differentiation of roothairs in the absence of ethylene (AVG treated) was very early compared with differentiation in the absence or presence of salt. Roothairs extend by adding new membranes at their tips (Chasan 1993), and it is also a way of increasing root radius. This morphological attribute appears to contribute to more absorption of water in response to high external salt concentration.

Other morphological features observed in our study with salt treatment include roots becoming deformed and nodules or "bumps" which appeared close to the apical region (Fig. 3). Salt treatment also caused reduction in epidermal cell length, which was more pronounced in the sensitive than the tolerant cultivar (Table 6). Morphometric analysis of cross-sections from the differentiation zone of soybean roots revealed a reduction of NaCl in the apoplast (compared to the cytoplasm) of salt-stressed roots which probably reflects an adaptive response to avoid NaCl loading (Hilal and

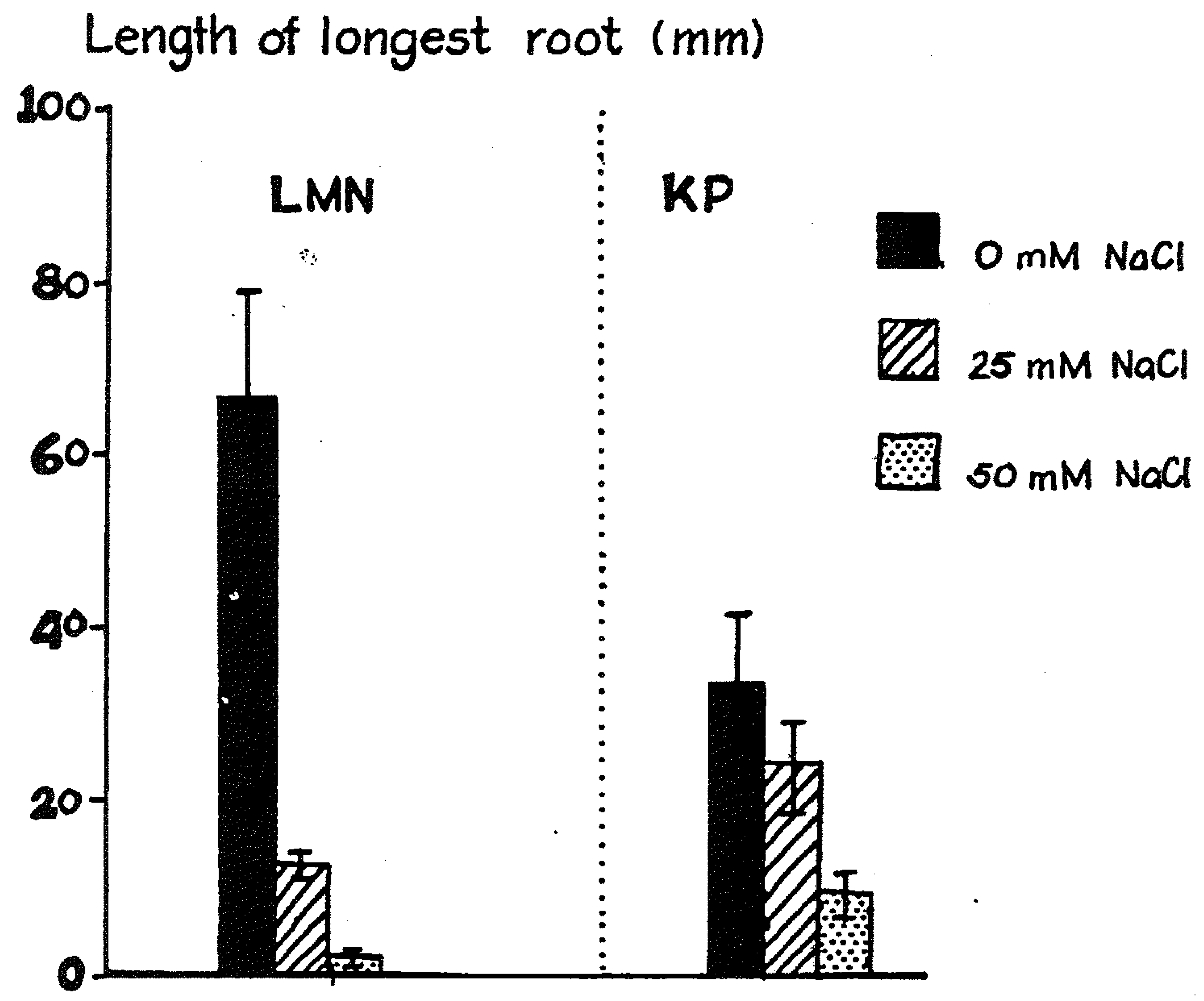

Fig. 2. The effect of NaCl on root elongation of a salt tolerant, KP, and sensitive, LMN, rice cultivar.

Table 6. Effects of 50 mM NaCl and ethylene inhibitor, AVG, on seedling root length and root apical characters in salt-tolerant 'KP' and salt-sensitive 'LMN' rice cultivars. Data are means of 20 measurements (Alejar and Davies 1995).

Parameter	Treatment	KP Tolerant Cultivar	LMN Sensitive Cultivar
Length of longest root (mm)	Water	36.6	64.9
	NaCl	9.9	2.4
	AVG	6.3	16
Meristem length (µm)	Water	599	639
	NaCl	396	198
	AVG	388	490
Root hair zone (µm)	Water	1583	2072
	NaCl	2099	1307
	AVG	1377	620
Epidermal cell length (µm)	Water	27	34
	NaCl	21	22

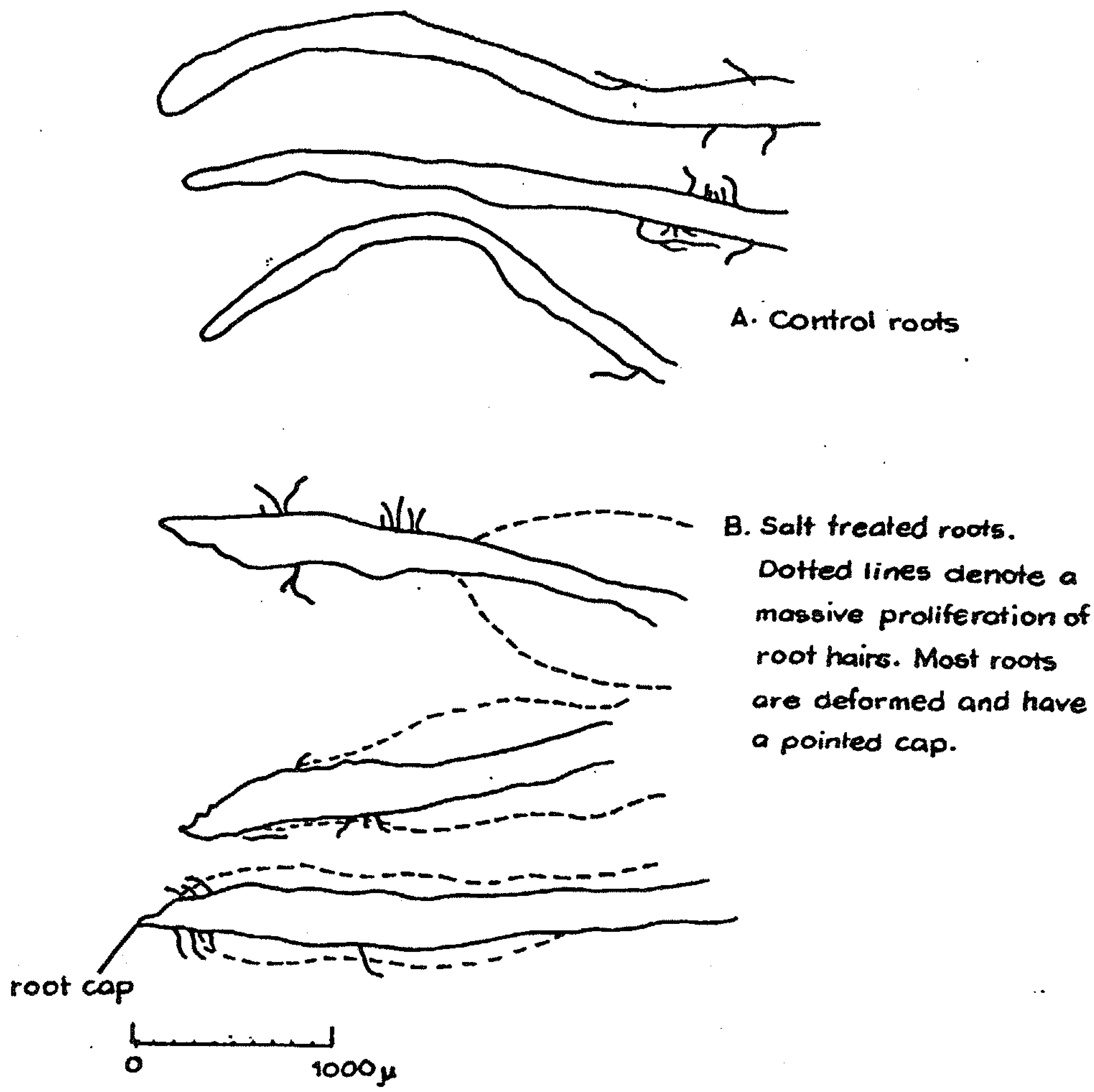

Fig. 3. Some morphological features of salt-stressed seedling root tips of rice

others 1998). Moreover, the same authors observed retardation of root primary xylem differentiation but secondary xylem development was induced by salt stress.

Proliferation of lateral roots was observed in our experiment on AVG-treated roots of both tolerant and sensitive cultivars. This effect is a common observation in stressed roots (Davies and others 1991; Cadiz 1995) and may arise as a result of the release of apical dominance in root tips known to be IAA-mediated and in our study, in the absence of ethylene. Again, this is likely an acclimation response of stressed roots, i.e., root cells retain their ability to divide and form root primordia. In older plants, these laterals or branch roots have extensive and complex vascular connections with main roots where carbon and nitrogen compounds from the root are recycled back to shoots (McCully 1995). In contrast, development of numerous adventitious and lateral roots caused by overproduction of IAA has been reported in *Arabidopsis*, superroot mutant (Boerjan and others 1995).

The stress imposed by salinity could be water stress due to the osmotic effects of the salt, or exerting toxic effects because of the ion excess and, hence, affecting a variety of metabolic activities. At toxic salt concentration, roots retain Na^+ and Cl^-, thus, preventing any salt-stress effects on shoots (Alejar and Erasga 1984) whilst osmoregulation via synthesis of new proteins is a well known acclimation to salt (osmotic) stress effect. Roots can accumulate a number of osmoprotective compounds in response to salt stress such as proline (Chou and others 1991) and polyamines (Krishnamurthy and Bhagwat 1989), or trehalose. The latter carbohydrate was found to be more important than proline in salt-stressed roots (Garcia and others 1997). Osmotic adjustment in salt stressed roots also involves compartmentation of proline and sucrose in cytoplasm and glucose and fructose in vacuoles as found in maize roots. Inorganic ions Na^+, K^+ and Cl^- contributed relatively more to solute potential than these organic solutes (Rodriguez and others 1997).

Compact Soil

Reduction in growth of seedling roots is more pronounced when grown in compact soil (Table 7), which may be due to mechanical impedance and restricted movement of air and water in soil. In our experiments, we used a soil type where moisture content was calibrated to be non-limiting and, hence, stress imposed is the high mechanical resistance of the soil. The growing roots during shoot emergence and root elongation are capable of exerting pressure greater than the mechanical resistance of the soil. Fig. 4 shows our results on soil-compacted roots of rice and alleviation of the stress by incorporating different concentrations of 2,4-D in the soil. The effect of mechanical stress of compact soil can be explained in terms of osmoregulation in expanding cells. A much lower reduction in dry matter production of roots was detected in soil-compacted grown roots of a rainfed cultivar in spite of its greater reduction in root length than the irrigated cultivar (Table 7). Roots can also acclimate to soil compaction by a change in its cation exchange capacity and nitrogen content. Data in Table 7 also indicate that the less adapted to high mechanical impedance in soil, i.e. irrigated cultivar, can increase the total N content in roots. This would likely increase the osmotic concentration of the cell. Also, when root growth is opposed by mechanical resistance, tissues release ethylene and some endogenous hormones (Wilkins 1976) which in one way or the other contribute to acclimation response of the stressed root. Ethylene can bring about shorter but swollen roots but because of the wider area of the roots, a greater volume of the restricted soil layer can be explored.

Table 7. Comparative response of growth and total nitrogen content of soil-compacted roots of irrigated IR-56 and rainfed Azucena rice cultivars.

Parameter	Rice Cultivar	
	IR-56	Azucena
Length (mm)		
loose	56.3	76.9
compact	14.1	13.3
Fresh weight (mg)		
loose	14.0	25.7
compact	8.2	15.4
Dry weight (mg)		
loose	2.6	3.9
compact	1.7	2.8
Total nitrogen (%)		
loose	1.5	1.5
compact	1.7	1.4

Nutritional Disorder

Under conditions of limiting nutrient availability, plant roots may influence the availability and uptake of mineral nutrients by different mechanisms. These include release of root exudates, protons, bicarbonate ions and ectoenzymes. Roots can also produce mucilage gumming soil particles together to insure good root-soil contact. An aluminum-induced increase in root surface pH as the first evidence for an Al-resistance mechanism has been recently reported (Degenhardt and others 1998). In the tip region, outward diffusion of oxygen is hardly restricted as mentioned earlier. Such O_2 loss can, however, effectively oxidize the rhizosphere and thus oxidize ions such as iron and/or detoxify reduced compounds. Nutrient acquisition therefore can be modified and/or improved by roots under conditions of low or high supply of nutrients, e.g., phosphorus, iron or aluminum.

Phosphorus deficiency alters root development and metabolism (Johnson and others 1996). Increased cellular levels of phosphatase can occur in response to low supply of phosphorus (Marschner 1995). In our study on phosphorus deficient-grown Azolla, roots tend to grow longer while phosphatase activity increases (Table 8). This latter response renders more phosphorus available, hydrolysis of phosphate esters thus releases inorganic P, observed particularly in tolerant species. Phosphorus-deficient-induced increase in phosphatase activity reported in rice was greater in a tolerant cultivar than in the sensitive ones (Zaini and Mercado 1985).

In beans, P-deficient plants demonstrate this high plasticity (or the ability to sense and respond to localized changes in P availability), i.e., changes in lateral branching, root and root hair elongation rate and root gravitropism (Lynch 1995). Indeed, phosphorus-efficient genotypes have a vigorous branched root system with large number of apices (Lynch and van Beem 1993). The relatively longer roots of P-deficient plants is a common observation in our hydroponic cultures of tomato and sunflower. In lupins, proteoid roots (short densely clustered lateral roots) are induced to form where phosphorus uptake per unit root length is increased (Marschner 1995). In both cases changes in the total volume and site of soil explored by the roots would occur. Further, proteoid roots exude large amounts of citrate which increase not only solubilization of phosphorus (Johnson and others 1996) but also of potassium from both calcareous and acid soils (Marschner 1995). Similar root excretion of organic acids (citrate and malate) to chelate aluminum has been recently reported using *Arabidopsis* mutant (Hilal and others 1998) as a mechanism for aluminum toxicity tolerance.

Stimulation of cyanide-insensitive respiration in phosphorus-deficient plants seems to reflect metabolic adaptation allowing respiration to proceed because it negates the necessity for adenylates and inorganic P (Theodoru and Plaxton 1993). The involved enzyme alternative oxidase has been shown to be localized in root apical meristem and in developing xylem of soybean (Hilal and others 1997). Meanwhile, roots of some species are fortunate to associate themselves or even in symbiotic relationship with some organisms, rendering the otherwise unavailable nutrients such as phosphorus, manganese or nitrogen.

In response to iron deficiency, most

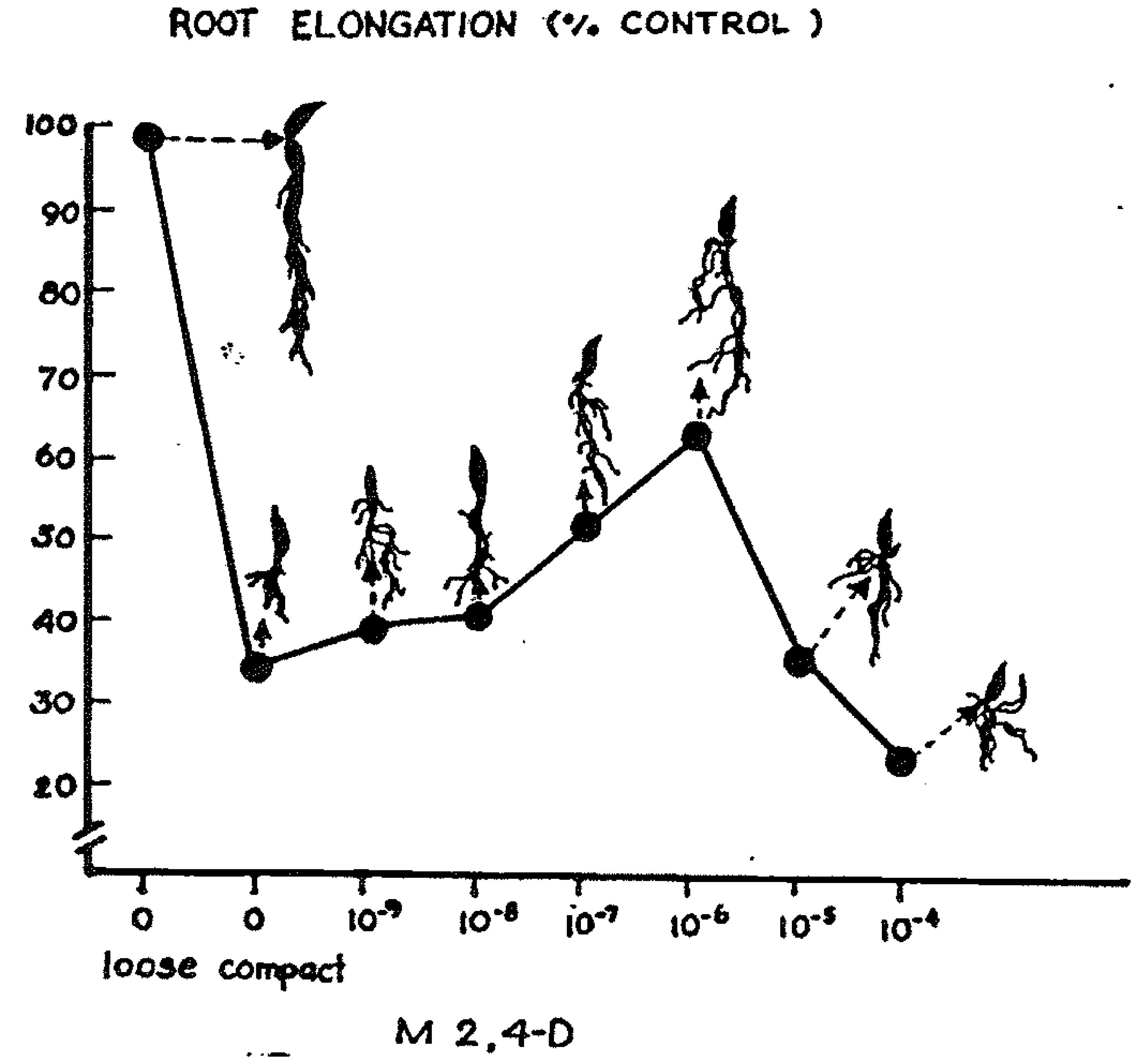

Fig. 4. A dose response curve on the effect of different concentrations of 2,4-D (incorporated in compacted (BD = 1.5 g cm^{-3}) soil) on root elongation of 6-day-old rice seedlings. Shoot growth is not shown

Table 8. Acid phosphatase activity of phosphorus-deficient tolerant and sensitive species of Azolla.

Azolla species/ External P Concentration	µmol-P-nitrophenyl phosphate/h/g dry weight
A. carolinia (304), tolerant	
5 ppm P	3.5
0 ppm P	52.5
A. pinnata (704), sensitive	
5 ppm P	15.1
0 ppm P	20.3

plant species in their apical root zones increase the rate of proton (H^+) net excretion or acidification (Schubert 1995; Hilal and others 1998), the reducing capacity, rate of Fe^{3+} reduction and iron uptake. Also, manganese reduction and uptake is increased seven-fold leading to high manganese concentration in iron-deficient plants (Marschner 1995). Roots of grass species release non-proteinogenic amino acids, phytosiderephores, which dissolve inorganic iron compounds by chelating Fe^{3+} and also mediate the plasma membrane transport of this chelated iron into the roots. Genotypic differences in release of phytosiderephores and uptake of iron phytosiderephores has been reported among graminaceous species (Romheld and Marschner 1990). Microbial siderephore, rhizoferrin, also mobilizes iron from soil minerals (Yoshida and others 1996). On the other hand, transport of heavy metals such as cadmium and zinc can be stimulated under iron deficiency (Cohen and others 1998). Similarly, we found that zinc-deficient plants contain high levels of Fe^{2+} and addition of zinc led to a marked reduction in iron concentration of shoot but not in roots (Table 9).

Roots growing in soil can also

Table 9. Effect of zinc supply on concentration of zinc and iron in roots and shoots of Zn tolerant, IR 34, and intolerant, IR 26, rice cultivars (Nicor 1994).

Zn concentration (ppm)	Zinc (ppm)				Iron (ppm)			
	IR-34		IR-26		IR-34		IR-26	
	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots
0	25	18	22	13	900	150	700	165
.05	60	21	55	16	995	135	758	150
0.10	1120	28	958	22	100	110	80	120
1.00	950	415	850	586	1375	82	1342	76
3.00	1500	500	1200	700	1480	72	1450	65

experience toxicity of excess of elements. Our investigation on Zn toxicity in hydroponically-grown rice (Nicor 1994) showed altered root growth and decreased root meristem size similar to previous reports on other species (Powell and others 1988; Davies and others 1991; Cadiz 1994). We also found that differentiation of xylem tissues was much later at high levels of Zn while very early at low levels. Root hair formation occurred nearer the root tip but surprisingly always farther than the first lignified xylem, in both cultivars with increasing (0 to 3 ppm) concentration of zinc. Anatomical observations revealed that toxic amounts of Zn resulted in wider diameter of xylem and thicker cortex in roots of the tolerant cultivar (Nicor 1994). Exclusion of toxic Zn by binding in the cell walls of roots (Cadiz 1995) renders the element unavailable to shoot and this can explain our results that the zinc tolerant IR-36 retained more of the element than the non-tolerant IR-26 (Table 9) which otherwise is toxic to the shoot. It is believed, however, that zinc sequestration in the vacuole is more important for zinc tolerance (Marschner 1995) than binding to cell walls.

Environmental Pollution

Environmental pollution arising from continuous burning of fossil fuels, oil, forest fires, harmful gas emissions and exhaust from industries all contribute greatly to rising global atmospheric carbon dioxide and thinning of the ozone layer. This phenomenon is associated with increase in temperature of the atmosphere. There are many reports on the effect of elevated CO_2 and temperature on growth of many crops. Initial results of our investigation, in collaboration with IRRI, revealed that seedling roots of 'NPT' grew longer (49%) at higher temperature than at ambient (Table 10). Increasing the ambient CO_2 by 200 $\mu l\ L^{-1}$ or temperature (plus 4 C) also improved root growth in NPT. High CO_2 can induce ethylene production (Alejar and others 1988b; Alejar and Brena 1998) and possibly favored root extension of NPT. However, with the addition of 300 $\mu l\ L^{-1}$ CO_2 at ambient or with high temperature, root growth was substantially reduced only in NPT, suggesting acclimation of this cultivar since there was no apparent effect on IR72 root growth. However, the number of roots in both cultivars appear to be

Table 10. Interactive effect of elevated CO_2 and temperature on root growth and meristem length of 7-day-old IR 72 ad NPT rice seedlings (Alejar and Macabata 1996).

Treatment	Rice Cultivar					
	IR-72			NPT		
	Length of Longest Root (mm)	Number of Roots	Meristem Length (μm)	Length of Longest Root (mm)	Number of Roots	Meristem Length (μm)
ambient CO_2 and ambient temperature	5.2	7.5	387	14.0	7.4	188
ambient CO_2 and ambient temperature + 4 C	5.2	9.1	287	20.4	8.4	192
ambient CO_2 + 200 μl L^{-1} CO_2 and ambient temperature	6.2	8.8	293	17.8	7.9	173
Ambient CO_2 + 200 μl L^{-1} CO_2 and ambient temperature + 4 C	5.9	9.5	220	21.6	7.7	162
Ambient CO_2 + 300 μl L^{-1} CO_2 and ambient temperature	3.2	5.0	112	5.6	7.5	112
Ambient CO_2 + 300 μl L^{-1} CO_2 and ambient Temperature + 4 C	4.6	7.2	84	4.6	6.8	124

unaffected by treatments. Microscopic examination of root tips revealed a greater meristem size of IR 72 than NPT. Table 11 also shows that meristem is reduced by CO_2 enrichment and/or high in both cultivars but reduction is more pronounced in IR72.

The present day atmosphere of increased UV-B radiation not only damages the shoot but also the roots. Reduction in elongation growth of seedling roots was 35% in a UV-B sensitive cultivar (Table 11) exposed to 19.1 kJ/m/day for 5 days. The damaging effect is more pronounced in the root meristem, where size was drastically reduced coupled with half the number of dividing cells compared with the controls. Examination of the teased cells of the meristem also revealed irregularly shaped and often broken cell walls. It is known that UV-B inactivates nucleic acids and proteins since both strongly absorb UV radiation. Root hairs differentiated earlier in UV-B sensitive cultivar 'Naizersail' than in the tolerant IR74. Acclimation response by roots to UV-B radiation is not presently known although in our study, we noted marked detachment of roots in UV-B exposed azolla UPLB Hybrid 1.

CONCLUSION

The relatively simple structure of roots, their diversity and developmental plasticity make them ideal for research. The success of responses of roots, the hidden half (Waisel and others 1991), to environmental stress has continuously intrigued plant scientists in agriculture, ecology and basic plant biology. Indeed, the more we learn about roots and how they work, the more complicated it becomes, yet the better able we understand control of plant growth and plant productivity in the field. Results of our studies on root apical characters indicate that it could be a useful selection criterion for stress tolerance in rice. Moreover, root tissues are ideal for dissecting genetic and molecular framework for many fundamental processes such as the identified gene loci for salt tolerance and on the comparative protein and RNA patterns of parent and inbred lines to explain salt tolerance.

Table 11. Effect of UV-B radiation in root length and root apical characters of UV-B sensitive 'Naizersail' and UV-B tolerant 'IR-74' rice cultivars

Parameters	UV-B level kJ m^{-2} d^{-1}	UV-B Sensitive Naizersail	UV-B Tolerant IR-74
root length	0	20.1	21.7
(mm)	19.1	15.2	14.1
meristem length	0	673	656
(µm)	19.1	520	539
root hair zone	0	354	301
(µm)	19.1	504	517
mitotic index	0	0.45	0.47
	19.1	0.23	0.26

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